

Role of Mechanosensory Stimuli in Intraspecific Agonistic Encounters of the Snapping Shrimp (*Alpheus heterochaelis*)

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Abstract. Intraspecific agonistic encounters in snapping shrimp (*Alpheus heterochaelis*) were analyzed using single-frame video analysis. The pair of conspecifics in such an encounter are designated as the snapper, which emits a fast water jet by very rapid closure, or snap, of the large modified snapper claw, and the receiver, which is the target of the water jet. The behavior of both snapper and receiver was evaluated before, during, and after the snap. Interactions between two intact shrimp (experimental series I) were compared with those between an intact shrimp and a “deprived” opponent (one with mechanosensory occlusion produced by coating the setae on the snapper claw with clear lacquer) (experimental series II). The behavior of the receiver is significantly changed by the occlusion, but that of the snapper is not. Intact and deprived opponents usually face each other during snapping, which is often preceded by touching of frontal appendages. The mean duration of claw cocking before snapping is about 500 ms. More than 50% of all snaps (and especially initial snaps) are directed towards the opponent, the water jet usually hitting the snapper claw of the receiver from a mean distance of 0.9 cm. Male shrimp show longer cocking durations, keep a shorter distance, and hit their opponents more often than do females. Intact and deprived snappers usually retreat immediately after snapping, but intact receivers usually approach. In contrast, deprived receivers retreat in most cases and show significantly prolonged latencies compared to intact receivers. Thus, mechanoreceptors on the snapper claw of the receiver play a significant role in intraspecific agonistic encounters.

Introduction

Agonistic encounters in competition for space, shelter, and access to mates or food are very common in crustaceans and have been studied extensively in different orders and families (Dingle, 1983; Hyatt, 1983) such as mantis shrimp (Stomatopoda; Caldwell and Dingle, 1975), freshwater prawns (Palaemonidae; Barki *et al.*, 1991), lobsters (Homaridae; Huber and Kravitz, 1995), crayfish (Astacidae, Cambaridae and Parastacidae; Copp, 1986; Söderbäck, 1991; Pavey and Fielder, 1996), and hermit crabs (Paguridae; Elwood and Neil 1992). Snapping shrimp differ from these crustaceans by having the ability to produce a rapid water jet, which is used in interactions with conspecifics and prey.

Alpheus heterochaelis, the big-clawed snapping shrimp of the family Alpheidae, which comprises about 425 species worldwide in subtropical and tropical oceans, reaches 5.5 cm in body length (Williams, 1984; Gruner, 1993). The animals used in this study originate from the Gulf of Mexico in northern Florida, where they live either individually or as heterosexual pairs in the littoral zone within oyster banks. Both sexes show a large, modified snapper claw on one (left or right) side, claw length reaching nearly half the body length, and a small pincer claw on the other side. Both claws are densely covered with setae of at least six different types (Read and Govind, 1991; Sullivan and Schmitz, 1997). The morphological differences between sexes include a broader pincer claw with fringes of plumoserrate setae on dactyl (movable finger) and propus in the male (Read and Govind, 1991), and a slightly broader abdomen with larger pleurites in the female (Nolan and Salmon, 1970).

In *Alpheus heterochaelis* the dactyl of the snapper claw possesses a huge stopper-like tooth (the plunger), which

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fits into a socket in the propus (Brooks and Herrick, 1891). Prior to snapping, the dactyl is cocked in a 100° position by cocontraction of claw opener and closer muscles, while the closer apodeme is lifted over a pivot point, so that tension is generated until a second closer muscle contracts (Ritzmann, 1974). During the following extremely rapid closure of the snapper claw (within about 1 ms; Schmitz and Herberholz, 1998) a short, very intense sound is produced (Knowlton and Moulton, 1963; Schmitz *et al.*, 1995) when the two claw surfaces hit each other. Furthermore, a rapid jet of water is formed when the dactyl plunger is driven into the propus socket, displacing water that escapes through a narrow anterior groove. Water jets elicited by slight tactile stimulation of the snapper claw in tethered animals show a well-focused main flow of water (width: about 30° at 3 cm distance) along an extension of the long axis of the snapper claw with maximum velocities of 3–10 m/s as revealed by flow visualization, high-speed video recordings, and laser Doppler anemometry (Herberholz and Schmitz, 1998; Schmitz and Herberholz, 1998).

Snapping can be used in offensive actions and to stun or even kill small prey such as grass shrimp and small pearl or goby fish (MacGinitie, 1937; MacGinitie and MacGinitie, 1949; Hazlett, 1962). In addition, by transferring hydrodynamic information toward the opponent via the water jet, snapping may warn the (usually conspecific) opponent not to enter an occupied shelter or territory. Intraspecific agonistic interactions in *A. heterochaelis* were previously studied by Nolan and Salmon (1970), Schein (1977), Conover and Miller (1978), and Hughes (1996a). In a thorough study of aggressive, submissive, and other acts in encounters between two snapping shrimp, Nolan and Salmon (1970) established general sequences of behaviors. Schein (1977) subsequently found that larger animals usually win, and that the eventually dominant shrimp displays more aggressive acts (*e.g.*, snaps). Chemical communication in *A. heterochaelis* was studied by Schein (1975) and Hughes (1996b), and the use of the cocked snapper claw as a visual signal was shown by Conover and Miller (1978) and Hughes (1996a); but the function of mechanosensory stimuli has not been studied previously.

The present paper is a quantitative analysis of the behaviors of the snapper shrimp and the receiver shrimp before, during, and after the snap. To understand the role of hydrodynamic stimuli in these interactions, we compared the responses of intact animals with those of snapping shrimp whose snapper claw had been occluded with clear lacquer.

This occlusion affects four types of setae, which have been morphologically described by Read and Govind (1991) as well as by Sullivan and Schmitz (1997), who also suggested possible functions for these setae. (1) Long

serrulate setae, up to 2.4 mm in length, show various types of serrulations and are found in groups (distally) or individually (proximally), especially near the lateral edges of the claw. These setae are usually loosely jointed at their bases and often show a preferential direction of movement; thus they are possible candidates for water jet reception and analysis. (2) Plumose setae, up to 1 mm in length, are restricted to the dorsal surface and are aligned along the closing edge of the propus. They may play a role in guiding and focusing the water jet. (3) Simple short setae, up to 0.1 mm in length, are evenly scattered over all the claw surfaces except the claw tip and the dactyl plunger. They appear to be fixed in a deep socket, and thus might represent contact mechanoreceptors. (4) Tubercles, which reach a diameter of 45 μm and a cone height of 35 μm , are restricted to three areas on the dorsal surface of the snapper claw. They are also thought to be contact mechanoreceptors.

The presence of these setae on the snapper claw suggests that occlusion of the claw might impede tactile interactions between the snapping shrimp and both production and reception of the water jet. Consequently, we have analyzed the behavior of intact and occluded shrimp during intraspecific agonistic encounters. Parts of the results have been published previously in abstract form (Schmitz and Iturrizaga, 1995; Herberholz and Schmitz, 1997a, b).

Materials and Methods

Forty adult snapping shrimp (*Alpheus heterochaelis*, length from rostrum tip to telson = 2.5–5.1 cm; 18 males and 22 females) were used in our behavioral experiments. Of these, 16 animals participated in encounters between two intact shrimp (experimental series I), and 24 different animals participated in encounters between one mechanosensorily deprived and one intact shrimp (experimental series II). The animals were caught among other snapping shrimp in waters of the gulf coast of Florida at the Florida State University Marine Laboratory in Sopchoppy and near Panacea. Prior to the experiments the animals were labeled with small numbers designed for marking queen bees and were kept individually in perforated plastic containers (11 × 11 × 15 cm) furnished with gravel and oyster shells for shelter. The containers were placed within a large tank (90 × 195 × 33 cm) with 330 l of circulating filtered seawater (salinity, 23–28‰; temperature, 22°–23°C). Proteins were removed from the water and pH, carbonate, oxygen, CO₂, and NO₃ were regularly controlled. The shrimp were exposed to an illumination cycle of 12 h light/12 h dark and fed frozen shrimp, fish, mussel, or *Artemia salina* three times a week.

Experiments were conducted within a 25 × 15 × 16 cm aquarium (water level, 8 cm; temperature, 22°C; floor, covered with black cloth to facilitate walking) on a platform

isolated from vibration (Breithaupt *et al.*, 1995). The short sides of the aquarium were covered with transparent paper, and two Schott KL 50 light guides on each side were used to enhance contrast for video recordings (average intensity = 50 lux). For mechanosensory occlusion the setae on the snapper claw of one shrimp were covered with clear lacquer (Pigrol Farben GmbH, Ansbach) while being viewed under a microscope. The intact opponent was treated in the same way, but did not receive the occlusion. Prior to the experiments two animals (both intact or one intact and one occluded, of the same or different sex) were placed in the aquarium for 10 min for acclimatization; the shrimp were separated by an opaque partition to prevent visual and tactile contact. After removal of the partition, all interactions between the shrimp were videotaped (camera, Panasonic AG 455; videorecorder, Panasonic AG 7355; monitor, Sony Trinitron) for 20 min from above and from the side by means of a mirror set at a 45° angle from the base of the aquarium. After each encounter with deprived animals the occlusion was reexamined, and behavioral data were evaluated only if the snapper claw was still completely covered with lacquer, which was true in the majority of cases. A snapping shrimp met the same conspecific only once and was usually tested no more than once a day. Seventy-two experiments with a total of 326 snaps were subsequently characterized using single-frame analysis (50 frames/s) and statistical procedures. Statgraphics Plus 6.0 and SPSS 6.0.1. were used for conventional statistics and circular statistics (Batschelet, 1981) for evaluating the mean vector direction, the angular deviation, and the length r of the mean vector.

For each animal, sex, body length, and snapper claw side, length, width, and thickness were determined in the living shrimp. Each snapping interaction was characterized by the latency between a preceding tactile interaction and the snap (disregarding durations of 5 s or more); the cocking duration, *i.e.* the time between completely opening the snapper claw (cocking the dactyl in a 100° position) and the beginning of claw closure; the distance between the opponents and the body alignment (head-head, head-tail, tail-head, tail-tail) during the snap; the goal of the snap; and the behavior and latency of both animals after the snap. The following angles were also measured:

1. The body axis angle β between the longitudinal body axes of the interacting animals (ranging from 0° to $\pm 180^\circ$, positive when ipsilateral to the snapper claw of the snapper and negative when contralateral to it; see Fig. 1A).

2. The position angle δ between the longitudinal body axis of the snapper and the line connecting the midpoints of both shrimp (range and sign definition as for the angle β ; see Fig. 1A).

3. The snapper claw angle γ between the snapper

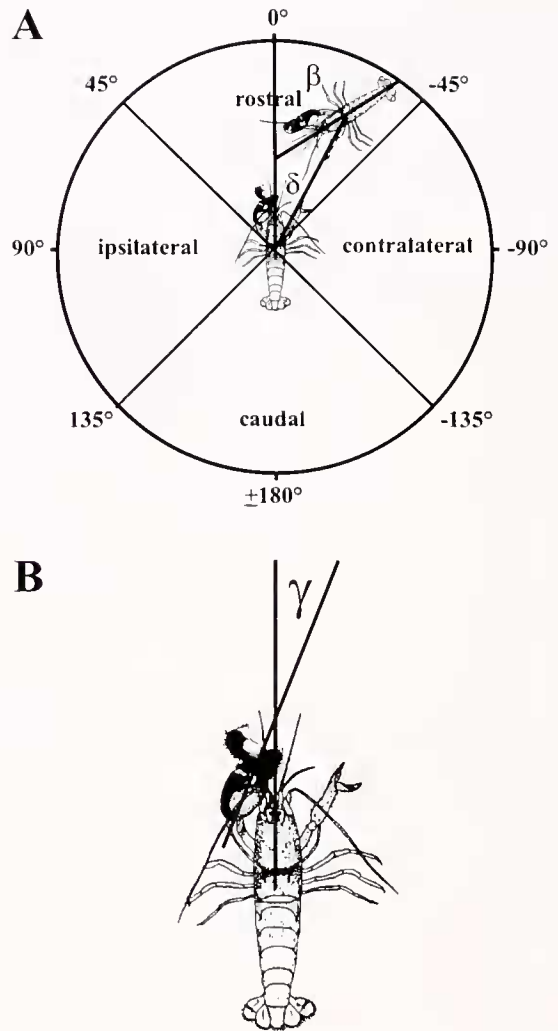


Figure 1. Definitions of the body axis angle β , the position angle δ , and the snapper claw angle γ in snapping shrimp interactions during snapping. (A) The body axis angle β is given by the angle between the longitudinal body axes of both animals, ranging from 0° to $\pm 180^\circ$; it is positive when ipsilateral to the snapper claw of the snapper and negative when contralateral to it. The position angle δ is given by the angle between the longitudinal body axis of the snapper and the line connecting the midpoints of both shrimp (range and sign definition as for β). (B) The snapper claw angle γ is given by the angle between the snapper claw long axis and the longitudinal body axis in the snapping animal; it is negative when crossing the animal's midline.

4. The tailfan angle with respect to the abdomen in the snapper (0°—fully folded, 90°—bent downwards, 180°—stretched out) during the snap.

Results

Our experiments with *Alpheus heterochaelis* were designed to compare the interactions of an intact snapping

shrimp and an intact conspecific (experimental series I) with the interactions of a snapping shrimp having an occlusion of the setae on its snapper claw and an intact conspecific (experimental series II). The deprived animal in experimental series II—like both intact shrimp in experimental series I—acted as the snapper, the receiver, or both during an experiment. Except for general characteristics, the behavior of the intact opponent in experimental series II was not analyzed; thus independent behavioral data are shown in most cases.

General characteristics and behavior before snapping

Intact shrimp produced an average of 3.4 ± 2.8 ($\bar{X} \pm SD$, $n = 218$) snaps per experiment towards each other (series I). Shrimp with an occluded snapper claw showed significantly fewer snaps per experiment ($\bar{X} \pm SD = 1.1 \pm 1.0$, $n = 45$) towards the intact opponent (Mann-Whitney U test: $P < 0.01$), but did not differ significantly from intact shrimp in the same series (II), which produced 1.6 ± 1.6 ($\bar{X} \pm SD$, $n = 63$) snaps per experiment towards them (Mann-Whitney U test: $P > 0.05$). In interaction experiments with two intact snapping shrimp, the mean body size of the snapping animal ($\bar{X} \pm SD = 3.7 \pm 0.8$ cm, $n = 218$) and the receiving animal ($\bar{X} \pm SD = 3.6 \pm 0.6$ cm, $n = 218$) did not differ significantly, which is also true for the body size of the snapper ($\bar{X} \pm SD = 4.0 \pm 0.2$ cm, $n = 108$) and the receiver ($\bar{X} \pm SD = 4.0 \pm 0.3$ cm, $n = 108$) in experiments with one mechanosensorily deprived shrimp.

To obtain information about the stimuli that elicit snapping, we analyzed the tactile interactions between the opponents before snapping occurred and measured the interval between the last contact and the snap, that is, the moment when the cocked snapper claw closed rapidly. Regardless of the condition of the snapper claw, frontal appendages (antennae, snapper claw, and pincer claw) were most frequently used in tactile interactions before snapping, while carapace, tailfan, and legs (summarized as B for "body") were less often contacted (Fig. 2A, B). There is a tendency for deprived animals—in comparison to intact ones—to be touched less often at the antenna and more often at the (occluded) snapper claw before snapping, and to be touched more often at the antenna before receiving a snap. However, χ^2 tests did not reveal any significant differences between intact or occluded snappers or receivers with regard to the touched body parts. The interval between touch and snap (disregarding durations of 5 s or more, which were rare) is 1.4 ± 1.1 s ($\bar{X} \pm SD$, $n = 169$) for intact snappers and 1.6 ± 0.8 s ($\bar{X} \pm SD$, $n = 29$) for mechanosensorily deprived snappers, and does not differ significantly (Mann-Whitney U test: $P > 0.1$) between these animals.

The cocking duration of the snapper claw before snap-

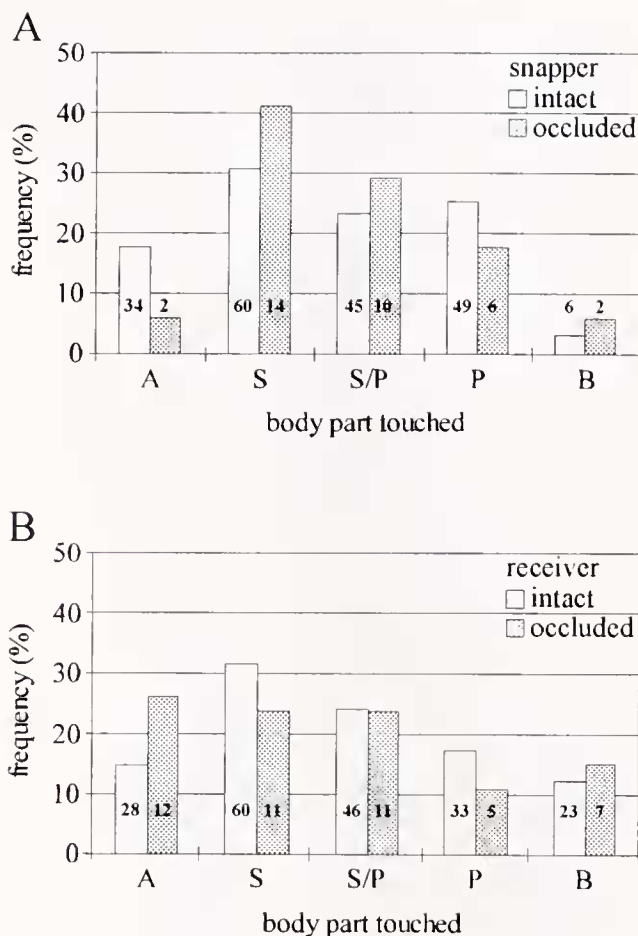


Figure 2. Frequency histogram of body parts of (A) the snapper and (B) the receiver touched by the opponent before snapping occurred in interactions between two intact animals (experimental series I, white columns) and in interactions of a shrimp with an occluded snapper claw and an intact shrimp (experimental series II; only data for the occluded animal are shown, dotted columns). A, antenna; S, snapper claw; S/P, snapper and pincer claw; P, pincer claw; B, body, *i.e.*, carapace, tailfan or legs. Here and in all following figures the numbers illustrate the numbers of observations.

ping (see Materials and Methods) is 513 ± 172 ms ($\bar{X} \pm SD$, $n = 193$) in agonistic encounters of intact shrimp and does not differ significantly (Mann-Whitney U test: $P > 0.1$) from the cocking duration of deprived snappers ($\bar{X} \pm SD = 532 \pm 136$ ms, $n = 37$). Cocking duration is not correlated with snapper claw length or body length.

Behavior during snapping

The snapper keeps its snapper claw parallel to its longitudinal body axis or slightly crossing the midline; the snapper claw angle γ is $-9.6^\circ \pm 15.4^\circ$ ($n = 203$, $r = 0.964$, circular statistics) for intact shrimp and $-0.9^\circ \pm 16.0^\circ$ ($n = 39$, $r = 0.960$, circular statistics) for deprived animals. The tailfan is usually kept at about a right angle

downward from the abdomen (circular mean for intact snappers: $73.6^\circ \pm 35.8^\circ$, $n = 205$, $r = 0.805$; circular mean for deprived snappers: $89.0^\circ \pm 41.0^\circ$, $n = 26$, $r = 0.750$), which simultaneously stabilizes the stance of the snapping animal and prepares it for escape after the snap (see below).

The body axis angle β between the longitudinal body axes of both animals during the snap is $7.8^\circ \pm 58.9^\circ$ ($n = 215$, $r = 0.471$, circular statistics) for intact shrimp and $8.9^\circ \pm 53.7^\circ$ ($n = 45$, $r = 0.558$, circular statistics) for shrimp with an occluded snapper claw (Fig. 3A). Thus, the distribution is rather symmetrical with respect to 0° in both cases. The absolute body axis angle $|\beta|$ is $44.8^\circ \pm 47.4^\circ$ ($r = 0.658$, circular statistics) for intact animals and $37.5^\circ \pm 44.8^\circ$ ($r = 0.690$, circular statistics) for deprived ones; that is, the longitudinal body axes of the interacting animals usually encompass small angles. The position angle δ between the longitudinal body axis of the snapper and the line connecting the midpoints of both animals is $2.4^\circ \pm 42.8^\circ$ ($n = 215$, $r = 0.721$, circular statistics) for intact snappers and $2.0^\circ \pm 29.6^\circ$ ($n = 44$, $r = 0.866$, circular statistics) for deprived snappers (Fig. 3A), and the absolute position angle $|\delta|$ is $29.1^\circ \pm 34.0^\circ$ ($r = 0.824$, circular statistics) for intact animals and $17^\circ \pm 24.9^\circ$ ($r = 0.905$, circular statistics) for deprived ones. Thus, regardless of the occlusion, the receiver is usually positioned in the rostral quadrant with respect to the snapper during the snap (see Fig. 1A). As illustrated in Figure 3A, small body-axis angles in combination with small position angles predominate in both cases. In addition, the shrimp usually face each other during the snap (h-h, head of snapper oriented towards head of receiver: 87% for intact animals, 89% for deprived animals); only rarely does the snapper face the tail of the receiver (h-t) or its tailfan closest to the receiver (t-h, t-t; Fig. 3B).

The distance between opponents during snapping is related to whether the snap is undirected or directed. In an undirected snap, the snapper claw of the snapper is not pointed toward the receiver. In a directed snap, the snapper claw is positioned so that the main flow of water (along an extension of the long axis of the claw; see Introduction) hits the receiver. The latter type, which is more frequent, occurs with shorter distances between the opponents (Fig. 4A). As shown in Figure 4A left, for directed snaps the distance between the tip of the snapper claw and the nearest body part of the receiver in extension of the snapper claw long axis is 0.9 ± 1.0 cm ($\bar{X} \pm \text{SD}$, $n = 117$, 54%) for intact shrimp and 0.9 ± 0.8 cm ($\bar{X} \pm \text{SD}$, $n = 25$, 56%) for mechanosensorily deprived animals. For undirected snaps (Fig. 4A right) the distance between snapper claw tip and the nearest body part of the receiver in any direction is 4.1 ± 3.0 cm ($\bar{X} \pm \text{SD}$, $n = 100$, 46%) for intact shrimp and 4.6 ± 4.2 cm ($\bar{X} \pm \text{SD}$, $n = 18$, 44%) for mechanosensorily deprived animals. Values for

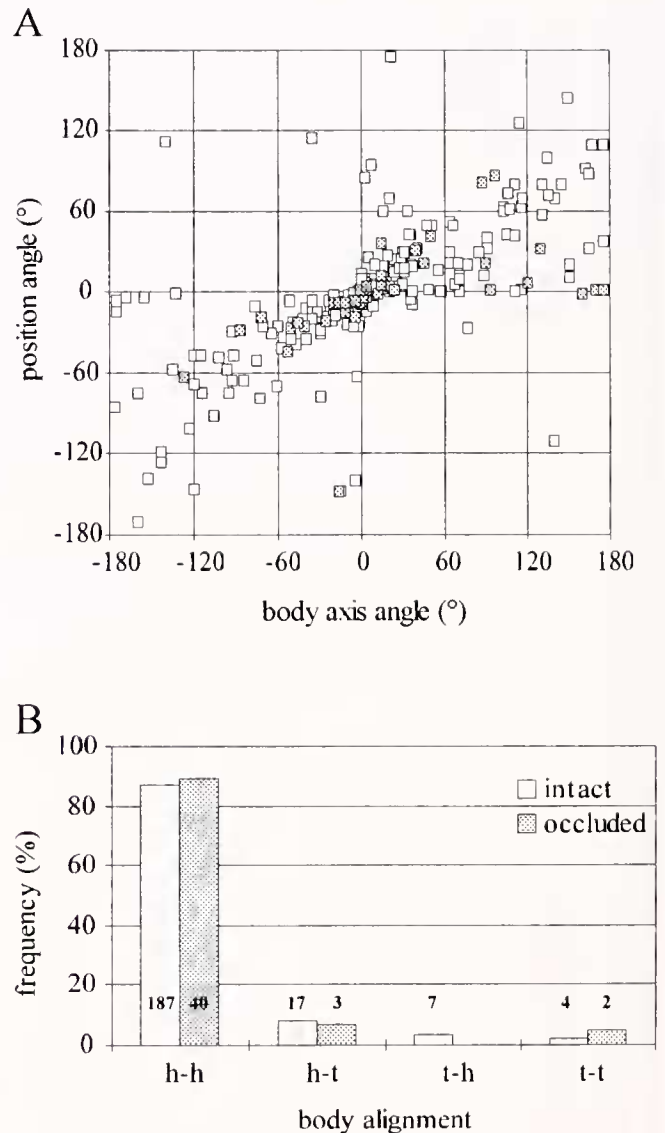


Figure 3. (A) Scatter plot of the position angle δ between the longitudinal body axis of the snapper and the line connecting the midpoints of both shrimp versus the body axis angle β between the longitudinal body axes of the opponents during snapping for intact shrimp (\square , $n = 215$) and animals with an occluded snapper claw (\blacksquare , $n = 44$); see Fig. 1 and text for definitions and details. (B) Frequency histogram of body alignments of both shrimp during the snap for intact shrimp (white columns, $n = 215$) and animals with an occluded snapper claw (dotted columns, $n = 45$). h, head, t, tail, first letter for the snapping animal and second one for the receiver; *i.e.*, h-t means that the head of snapper is closest to the tail of receiver.

intact and mechanosensorily deprived animals do not differ significantly (Mann-Whitney U test: $P > 0.5$), whereas in both groups of animals the mean distance for directed snaps is significantly smaller than that for undirected snaps (Wilcoxon test, $P < 0.01$ or < 0.05 , respectively). In interactions between intact snapping shrimp and in

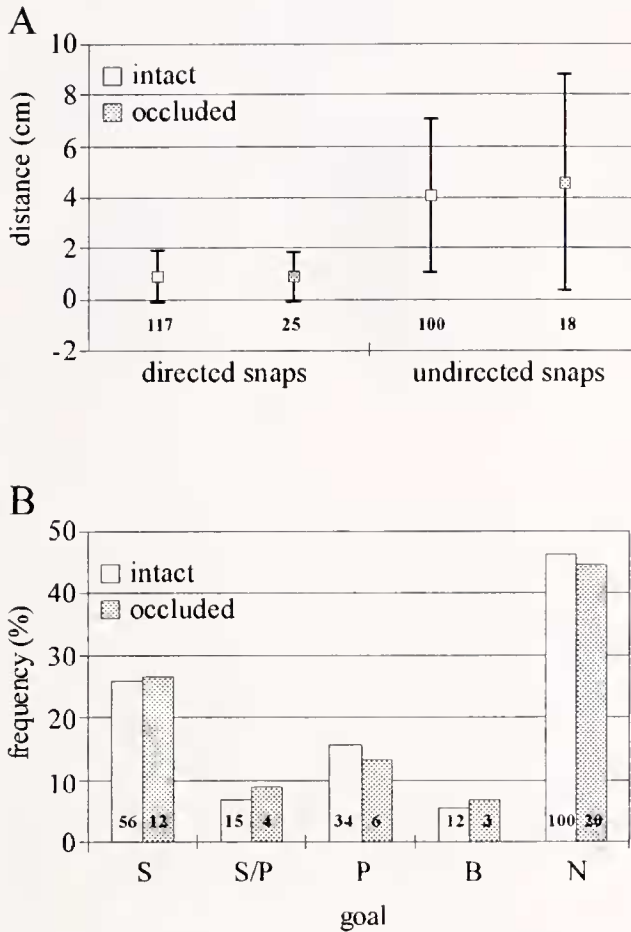


Figure 4. (A) Distance between opponents for intact snapping shrimp (open symbols) and animals with an occluded snapper claw (dotted symbols) during directed (left) and undirected (right) snaps. Values are means \pm SD. (B) Frequency histogram of the goal, i.e., the receiver body part first hit by the water jet of the snapping animal for intact shrimp (white columns) and animals with an occluded snapper claw (dotted columns). S, snapper claw; S/P, between snapper and pincer claw; P, pincer claw; B, body, i.e., carapace, tailfan or legs; N, none.

those between a shrimp with an occluded snapper claw and an intact animal, the goal of the directed snap is usually either the snapper claw or (less often) the pincer claw (Fig. 4B), both of which are densely covered with setae in intact animals. The area between the claws and other body parts is hit less often.

In our experiments, 30 snaps of intact snapping shrimp and 4 snaps of shrimp with an occluded snapper claw (initial snaps) were immediately (within 1 s) followed by a return snap of the opponent. In 3 of the 30 cases in experimental series I, the exchange of snaps was followed by a second snap from the initial snapper. As shown in Figure 5A (white columns), in intact snapping shrimp, initial snaps were more often directed towards the receiver; that is, they hit it more often (24 out of 30, 80.0%)

than return snaps (16 out of 30, 53.3%) and other snaps (77 out of 157, 49.0%). Similarly, as shown by the dotted columns in Figure 5A, all initial snaps of mechanosensorily deprived shrimp hit the receiver (4 out of 4, 100%), while subsequent snaps were less accurate (return snaps: 3 out of 8, 37.5%; other snaps: 18 of 33, 54.5%).

Averaging the distances for directed and undirected snaps reveals that for intact snapping shrimp the mean distance progressively increases from initial snaps ($\bar{X} \pm \text{SD} = 0.8 \pm 1.0$ cm, $n = 30$) to return snaps ($\bar{X} \pm \text{SD} = 1.7 \pm 1.6$ cm, $n = 30$) and to the other snaps ($\bar{X} \pm \text{SD} = 2.8 \pm 3.0$ cm, $n = 157$) with significant differences for initial and return snaps *versus* the remaining snaps (Wilcoxon test, $P < 0.05$, open symbols in Fig. 5B). For mechanosensorily deprived shrimp (dotted symbols in Fig. 5B) the mean distance for initial snaps amounts

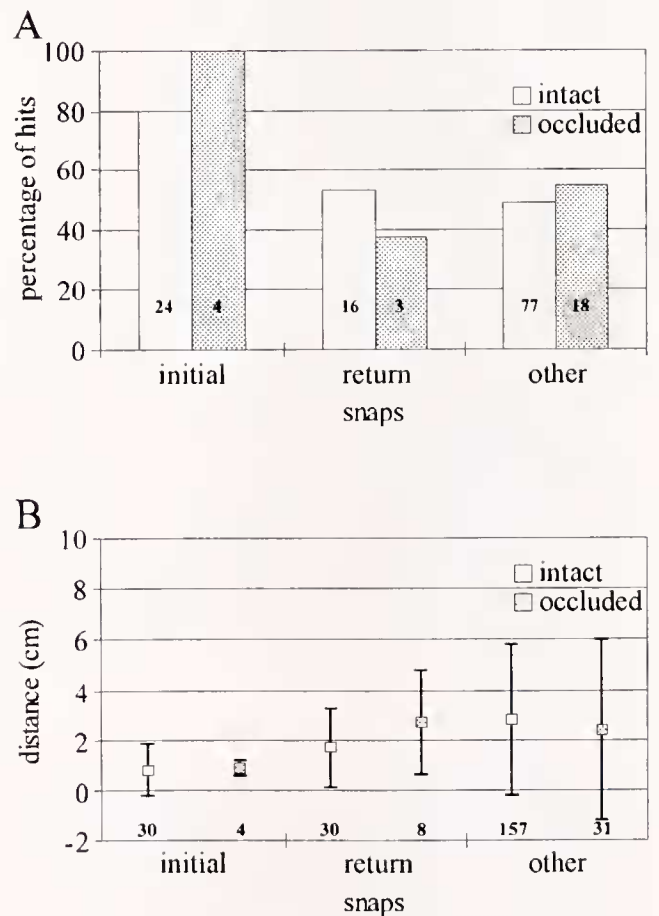


Figure 5. Comparison of different snap types. (A) Percentage of hits, i.e., of snaps directed towards the opponent, for initial snaps, return snaps, and the remaining snaps in intact shrimp (white columns) and animals with an occluded snapper claw (dotted columns). Numbers illustrate the numbers of hits. (B) Mean distance and standard deviation between the tip of the snapper claw of the snapping animal and the receiver for the three snap types in intact animals (open symbols) and mechanosensorily deprived shrimp (dotted symbols).

to 0.9 ± 0.3 cm ($\bar{X} \pm SD$, $n = 4$) and is lower than for return snaps ($\bar{X} \pm SD = 2.7 \pm 2.1$ cm, $n = 8$) and for the other snaps ($\bar{X} \pm SD = 2.4 \pm 3.6$ cm, $n = 31$).

Agonistic encounters between snapping shrimp were also analyzed with respect to the sex of the snapping animal. We analyzed 14 female/female, 5 male/male, and 13 female/male experiments from experimental series I (with two intact snapping shrimp) and 6 female/female, 8 male/male, and 14 female/male experiments from experimental series II (with one mechanosensorily deprived and one intact snapping shrimp).

As shown in Figure 6A, the percentage of hits (*i.e.*, of directed snaps) is significantly higher in males than in females (intact males: 52 of 79, 65.8%; intact females: 65 of 138, 47.1%; occluded males: 17 of 25, 68.0%; occluded females: 8 of 20, 40.0%; χ^2 tests, $P < 0.01$ for intact animals and < 0.05 for mechanosensorily deprived shrimp). In addition, as shown in Figure 6B, snapping distances of intact male snappers ($\bar{X} \pm SD = 1.6 \pm 2.2$ cm, $n = 79$) are significantly shorter than those of intact female snappers ($\bar{X} \pm SD = 2.8 \pm 2.9$ cm, $n = 138$) (Mann-Whitney U test: $P < 0.01$). The snapping distance of occluded males ($\bar{X} \pm SD = 1.9 \pm 3.3$ cm, $n = 24$) shows a trend towards being smaller than that of occluded females ($\bar{X} \pm SD = 2.8 \pm 3.1$ cm, $n = 19$), but does not differ significantly (Mann-Whitney U test: $P > 0.2$). As shown in Figure 6C, the mean cocking duration of intact males ($\bar{X} \pm SD = 583 \pm 173$ ms, $n = 66$) significantly exceeds that of intact females ($\bar{X} \pm SD = 477 \pm 160$ ms, $n = 127$) (Mann-Whitney U test: $P < 0.01$), whereas the difference between the cocking duration of occluded males ($\bar{X} \pm SD = 540 \pm 164$ ms, $n = 21$) and that of occluded females ($\bar{X} \pm SD = 521 \pm 82$ ms, $n = 16$) is not statistically significant (Mann-Whitney U test: $P > 0.6$). Thus, in intraspecific agonistic encounters, snapping shrimp exhibit sex-specific differences: males show a longer cocking duration than females, keep a shorter distance to the receiver during snapping, and hit it more often.

Behavior after snapping

In interactions between two intact animals, the first behavioral response after *directed* snaps differs remarkably between the snapper and the receiver (*cf.* white columns in Fig. 7A and 7B). The intact snapper usually retreats, *i.e.* either tailflips or withdraws more slowly (73.9% of the cases); less often it does not change its behavior (13.0%) or even approaches the receiver (13.0%). In contrast, the intact receiver usually approaches the snapper (51.3% of the cases); more rarely it retreats (28.2%) or does not change its behavior (20.5%). Intact snappers thus retreat significantly more often than intact receivers (Wilcoxon test, $P < 0.05$), and the latter

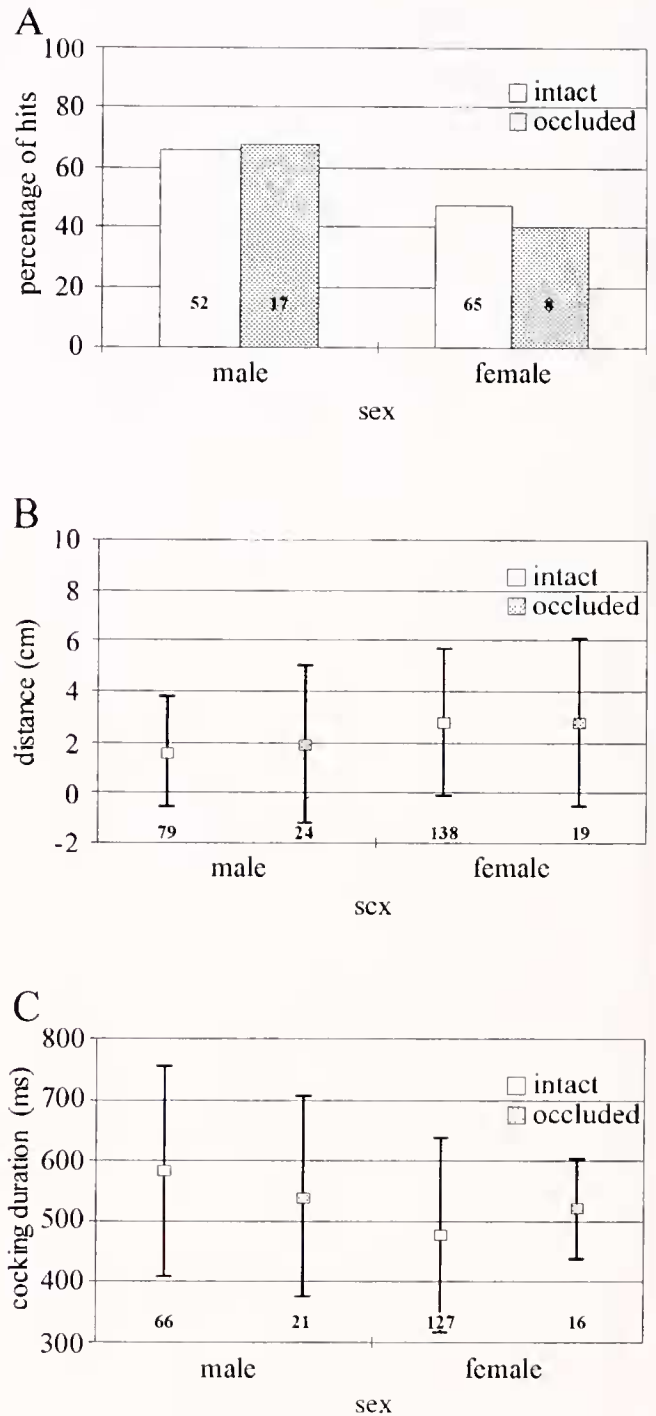


Figure 6. Comparison of male and female behavior before and during snapping. (A) Percentage of hits, *i.e.*, of snaps directed towards the opponent, (B) mean distance and standard deviation between the tip of the snapper claw of the snapping animal and the receiver, and (C) mean cocking duration and standard deviation for intact (white columns and open symbols) and mechanosensorily deprived (dotted columns and symbols) males (left) and females (right). *Cf.* Fig. 5.

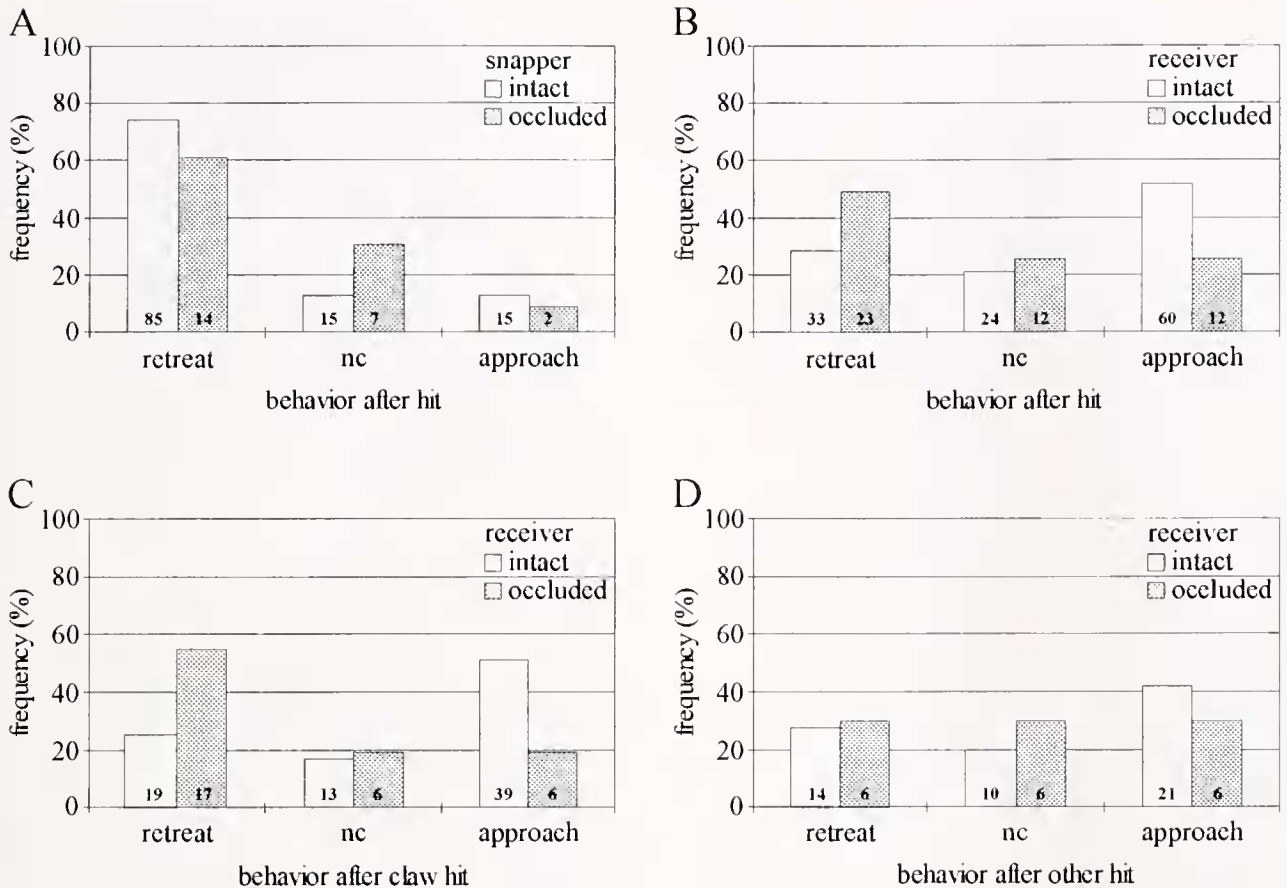


Figure 7. Frequency histograms of behaviors after directed snaps in the snapper (A), in the receiver (B), in the receiver after the snapper claw was hit (C), and in the receiver after other body parts were hit by the water jet (D); nc, no change. Data for intact animals are illustrated by white columns, data for shrimp with an occluded snapper claw by dotted columns.

approach significantly more often than intact snappers (Wilcoxon test, $P < 0.01$).

As illustrated in Figure 7A, the behavior of snappers with an occluded snapper claw (dotted columns) does not differ significantly from that of intact snappers (white columns; χ^2 test: $P > 0.1$). Deprived snappers likewise usually retreat (60.9% of the cases), less often do not change their behavior (30.4%), and only rarely approach the receiver (8.7%). Receivers with an occluded snapper claw, on the other hand, differ significantly (χ^2 test: $P < 0.01$) from intact receivers in their behavior after being hit by the water jet (Fig. 7B). They retreat in most cases (48.9%—more often than intact receivers), approach the snapper less often (25.5%) than intact ones, and show no change in their behavior somewhat more frequently (25.5%). It can be shown that this behavior is a result of snapper claw occlusion, since these animals exhibit a significant behavioral change (χ^2 test: $P < 0.01$, Fig. 7C) only when the water jet hits the snapper claw (goal = S or S/P, cf. Fig. 4B); when they

are hit on other body parts they behave like intact receivers (χ^2 test: $P > 0.5$; Fig. 7D).

Latencies between the directed snap and the first behavioral response are significantly higher for receivers than for snappers (Mann-Whitney U tests: $P < 0.01$ each for intact and mechanosensorily deprived snapping shrimp; Fig. 8A). In addition, latencies of deprived snappers ($\bar{X} \pm \text{SD} = 49 \pm 70$ ms, $n = 13$) are significantly higher than those of intact snappers ($\bar{X} \pm \text{SD} = 29 \pm 73$ ms, $n = 98$, Mann-Whitney U test: $P < 0.01$; Fig. 8A left), though the difference is small when considering the 20-ms resolution of the single-frame video analysis. Furthermore, deprived receivers show significantly higher latencies ($\bar{X} \pm \text{SD} = 156 \pm 190$ ms, $n = 34$) than intact receivers ($\bar{X} \pm \text{SD} = 41 \pm 75$ ms, $n = 90$, Mann-Whitney U test: $P < 0.001$; Fig. 8A right). It can be shown that this extremely prolonged latency is mainly due to occlusion of the snapper claw. In comparison to intact receivers, deprived snap receivers react with significantly higher latencies when being hit on the occluded snapper claw

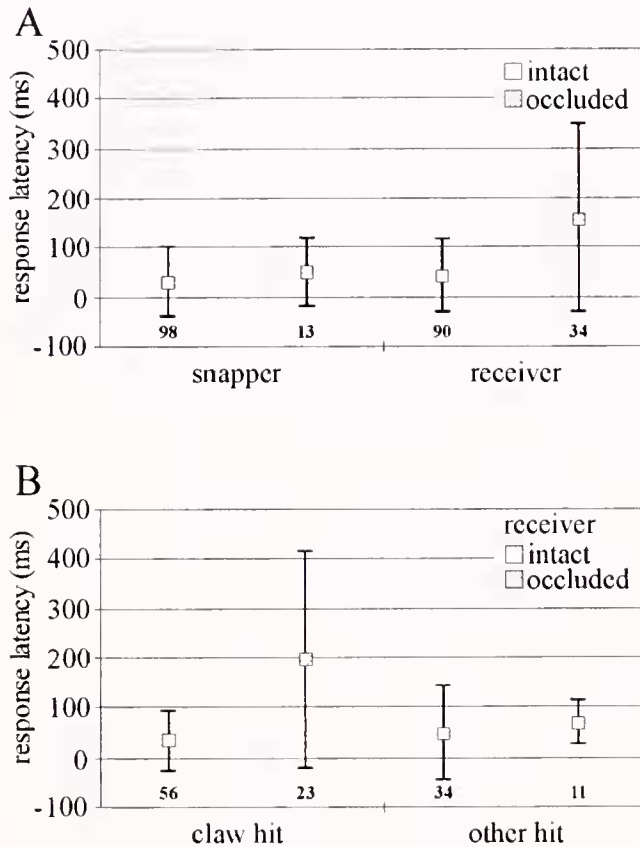


Figure 8. Response latency (means and standard deviations) after directed snaps in snappers (A, left) and receivers (A, right), in receivers after snapper claw hits (B, left), and receivers after hits of other body parts (B, right). Data for intact animals are illustrated by open symbols, data for shrimp with an occluded snapper claw by dotted symbols.

(intact: $\bar{X} \pm \text{SD} = 35 \pm 61$ ms, $n = 56$; occluded: $\bar{X} \pm \text{SD} = 197 \pm 219$ ms, $n = 23$; Mann-Whitney U test: $P < 0.01$; Fig. 8B right). There are also significant differences when other body parts are hit (intact: $\bar{X} \pm \text{SD} = 51 \pm 95$ ms, $n = 34$; occluded: $\bar{X} \pm \text{SD} = 71 \pm 44$ ms, $n = 11$; Mann-Whitney U test: $P < 0.05$; Fig. 8B left); however, here again the absolute difference is rather small.

These results show that snapping shrimp strongly depend on the mechanosensory system in intraspecific agonistic encounters. Intact mechanosensory equipment on the snapper claw is of great importance for snap receivers, while snapper claw occlusions have no effect, apart from slightly increased response latencies, on the behavior of the snapper.

Discussion

Snapping shrimp produce a fast, well-focused water jet by rapidly closing their large modified snapper claw, which is used in defensive and offensive interactions with conspecifics and prey. We quantitatively analyzed intra-

specific agonistic interactions between adults of the snapping shrimp species *Alpheus heterochaelis* to gain insights in the mechanisms of detection, identification, and localization of the opponent; the preparations for snapping (such as the approach and alignment of both shrimp, the positioning and cocking of the snapper claw); the snap itself (including the goal of the water jet); and finally the behaviors of both animals after the snap (approach and return snap, retreat, etc.). Our comparison of intact snapping shrimp and shrimp whose snapper claw had been occluded with clear lacquer did not reveal significant differences in the behavior of the two groups before and during snapping, but mechanosensorily deprived snap receivers differed significantly from intact shrimp in their behavior after receiving a snap. These issues are discussed in the following sections.

Behavior before and during snapping

Body alignment. The sequence of events during agonistic interactions of two snapping shrimp (*Alpheus heterochaelis*) starts with the approach of the animals as described by Nolan and Salmon (1970). At this point the shrimp might be aware of each other by visual, hydrodynamic, or chemical information. The opponents align their body axes during the approach. Shortly before snapping, the shrimp are thus facing each other in most cases: the receiver is usually situated in the rostral quadrant with respect to the snapper, and the body axes of both mostly encompassing small angles (Fig. 3). This alignment does not differ in intact shrimp and animals with an occluded snapper claw. Thus, any hydrodynamic receptors on the snapper claw (long serrulate setae; see Introduction) do not play an essential role in the alignment of the shrimp.

Tactile interactions. The reduced distance between the animals allows additional tactile interactions, which (when disregarding durations of 5 s or more) occurred about 1.5 s before the snap. The short latencies indicate that most snaps were actually elicited by the tactile stimulus, especially in view of the 0.5-s duration of snapper claw cocking, which is included in these latencies. The last contact before snapping predominantly involves frontal appendages, with the overall touch frequency for intact and occluded snappers and receivers decreasing from the snapper claw to both claws to the pincer claw to the antennae (Fig. 2). These tactile interactions include active antennal probing—see also the mutual antennulation mentioned by Nolan and Salmon (1970)—and active claw probing. Thus, contact mechano- and chemoreceptors on the antennae and claws are presumably stimulated in these interactions, which can provide information for the localization and recognition of the opponent. Shrimp with an occluded snapper claw do not differ significantly from intact animals in this behavior, indicating that the

presence of mechanoreceptors (long serrulate setae, simple short setae, and tubercles) or chemoreceptors on the snapper claw is not essential in this process.

Claw cocking. In the next step of the encounter, one of the opponents starts to cock the dactyl of its snapper claw in a 100° position. While cocking this claw the snapping animal usually shields its frontal body parts by keeping the claw slightly across the midline. Thus, the snapper claw represents not only a weapon but also a protective device (apart from its function in the analysis of received water jets—see below). During the cocking of the snapper claw, tension is built up by cocontraction of a claw opener and a claw closer muscle (Ritzmann, 1974). Release of this tension produces extremely rapid claw closure with a mean velocity of about 6 m/s (Schmitz and Herberholz, 1998), generating a water jet of similar initial velocity. The duration of cocking in our experiments ranged, on average, from 510 to 530 ms, did not depend on the claw or body size of the shrimp, and was significantly longer in males than in females (Fig. 6C). In addition, cocking duration did not change significantly after occlusion of the setae on the snapper claw; thus the clear lacquer, which covered the entire snapper claw surface except for the dactyl plunger, did not impede the cocking mechanism. Interestingly, the velocity of the water jet did not increase systematically with the cocking duration, but flow visualization, high-speed video recordings (1000 frames/s), and laser Doppler anemometry showed that the jet velocities were highest after cocking durations of about 550 ms (Herberholz and Schmitz, unpubl. data). Therefore, according to our measurements of cocking duration, males should produce faster water jets than females, and intact and mechanosensorily deprived shrimp should, on average, both show optimal cocking durations.

Snapping frequency. The number of snaps per experiment in deprived shrimp was significantly lower than in intact shrimp facing intact opponents (experimental series I), but did not differ significantly from that of the intact animals in the same experiment (experimental series II). This might be caused by a different snapping motivation in the animals of the two experimental series. On the other hand, snapping in mechanosensorily deprived shrimp might be reduced by the lack of information about the water jet of the intact opponent (see below), who in turn reduces its own snapping frequency, thereby saving energy in the interaction with a less aggressive and thus presumably subordinate opponent. The snapping frequency certainly influences the success of a shrimp in intraspecific interactions. Conover and Miller (1978) immobilized the snapper claw dactyl in *Alpheus heterochaelis* and showed that these shrimp—no longer able to snap—could not compete successfully with intact individuals in acquiring or holding a shelter.

Goal of water jets. As was mentioned by Volz (1938)

in an early study of *Alpheus dentipes* and *Synalpheus laevimanus*, the snapping sound may merely represent a side effect of the rapid claw closure. Furthermore, auditory organs have not been detected in snapping shrimp. We thus suppose that the water jet is analyzed by the receiving shrimp and that mechanosensory sensilla are used to analyze these hydrodynamic signals.

More than 50% of all snaps are directed towards the opponent. The percentage of hits is increased for initial snaps, which appear to be better prepared than return or other snaps (Fig. 5A), as well as for snaps produced by males as compared to females (Fig. 6A). Directed snaps of intact and mechanosensorily deprived snappers usually hit the receiver on its snapper claw (Fig. 4B), an accessible target because of the "face-to-face" alignment of the shrimp (Fig. 3), the large size of the snapper claw, and in case of return snaps, the fact that this claw usually shields the frontal body parts during the preceding snap. On the basis of their morphology and distribution, the long serrulate setae on the snapper claw are good candidates for a role in the analysis of water jet velocity and direction (Sullivan and Schmitz, 1997). However, the velocity of the water jet is so high at short distances that other receptors such as the simple short setae and even the tubercles (supposed contact mechanoreceptors) might also respond to this strong stimulation.

Interindividual distance and water jet velocity. The amplitude of the hydrodynamic signal at the receptors of the receiver depends on the intensity of the signal as well as on the angle and distance between the sender and the receiver. The average interindividual distance for directed snaps of both intact and mechanosensorily deprived snappers is 0.9 cm—significantly smaller than for undirected snaps (Fig. 4A). According to flow visualization experiments videotaped at 1000 frames/s, water jets produced by animals with a large snapper claw (more than 2 cm in length) cover the distance of 0.9 cm within 2.0 ms, and the velocity of the jet is 2.1 m/s when it reaches the target (Herberholz and Schmitz, 1998). In spite of these high velocities, obvious damage to the receiving shrimp has not been observed. Furthermore, the reception of a water jet does not impede the behavior of an intact receiver, since in a first response it usually does not retreat, but rather approaches the snapper (Fig. 7B) and may even launch a return snap. On the other hand, small sympatric crabs (*Eurypanopeus depressus*), which represent a prey or a competitor for *Alpheus heterochaelis*, are attacked with a water jet from even shorter distances (on average 0.3 cm) than conspecifics and can be physically injured by this jet (Schultz *et al.*, 1998). Thus, we conclude that snapping in intraspecific encounters in *A. heterochaelis* is not used to damage the opponent, but that water jets can be viewed as threat displays that allow the receiver to assess the strength, fighting ability, and possibly other

characteristics of the snapping animal. These results agree well with those of Knowlton and Keller (1982), who showed that in the snapping shrimp *Alpheus armatus*, physical damage sustained during intraspecific fights does not result from water jets during snapping but from direct contact between the animals.

Sex-specific differences in snapping. If transfer of hydrodynamic information rather than damage is the main function of the snapping behavior, sex-specific characteristics of the water jet should also be important. In *Alpheus heterochaelis*, the male has a larger snapper claw than a female of equal size, and the female in field-caught pairs is usually larger in body size, which increases her egg-carrying capacity (Nolan and Salmon, 1970; Schein, 1975; Hughes, 1996a). In sexually selected species, males usually are more aggressive than females. Although *A. armatus* is an exception to this rule (Knowlton and Keller, 1982), *A. heterochaelis* conforms to it. One example of the female's lower aggressiveness in this species comes from laboratory experiments (Conover and Miller, 1978) in which two females were more likely than two males to co-occupy a shelter. Furthermore, in our experiments, the males showed longer cocking durations, snapped from smaller distances, and hit the opponent more frequently than the females did (Herberholz and Schmitz, 1997b; Fig. 6). Thus, the magnitude of the male's cocking durations and the timidity of the female (which prevents her from getting close to the opponent before snapping) both lead to higher water jet velocities at the receptor site when the signal is produced by a male shrimp. In this way hydrodynamic information allows the shrimp receiving the water jet to identify the sex of its conspecific opponent, provided that the distance of the opponent is also perceived (e.g., visually). In addition, visual, chemical, or tactile cues may be used for sex recognition. Hughes found that the female of *A. heterochaelis*, in contrast to the male, does not assess the size of its opponent on the basis of the open-claw display (Hughes, 1996a) and also does not distinguish between male or female chemical cues (Hughes, 1996b). On the other hand, Jeng (1994) showed that distant chemoreception using the antennular flagella plays an important role in sex recognition and pairing in the snapping shrimp *A. edwardsii*.

Behavior after snapping

Although snaps not aimed at the opponent (i.e., undirected snaps) may also produce perceivable hydrodynamic signals, we restricted our analysis to the behavior of the snapper and the receiver after directed snaps. Intact snappers usually retreat whereas intact receivers usually approach the opponent (Fig. 7A, B), the receiver latency slightly exceeding that of the snapper (Fig. 8A). Thus, the retreat of the snapping animal might not be a response

to the approach of the receiver but rather an action that was initiated before the snap by bending the tailfan downward. On the other hand, the snapper might receive a rebound of its water jet from the snapper claw of the opponent, which in turn stimulates its own mechanosensory system and induces the withdrawal. The retreat of the snapper increases the distance between the opponents, which is compensated for by the approach of the receiver. About 24% of these approaches were followed within 1 s by a return snap of the receiver; for these cases the retreat of the initial snapper represents an evasive strategy, while the receiver by approaching increases its chances to hit the opponent more strongly. Only rarely are return snaps answered immediately by a second snap of the initial snapper. This can be explained by the high energetic costs of snapping—or at least we know that the intensity of the acoustic signal decreases in a series of successive snaps (Schmitz *et al.*, 1995), and we suppose that the same is true for the velocity of the water jet.

The behavior of receivers with an occluded snapper claw differs significantly from that of intact receivers. Deprived receivers predominantly show the withdrawal behavior that is characteristic for snappers (Fig. 7A, B), and this is especially true when the water jet hits the occluded snapper claw (Fig. 7C). These findings show that hydrodynamic receptors on the snapper claw (presumably the long serrulate setae) play an important role in analyzing the water jet. These receptors are suited to transmitting information about the frequency, the amplitude, and the direction of the hydrodynamic signal. Once this information is missing, the opponent cannot be assessed and localized properly, and it is safer for the deprived shrimp to withdraw. Animals with an occluded snapper claw in general show increased latencies in their behavior (Fig. 8A, B). The largest latencies, however, are shown by deprived receivers—especially when the snapper claw is hit. Thus, although different mechanoreceptors may also be used to analyze the water jet, receptors on the snapper claw—the body part that is most exposed and hit first and often—certainly are essential in guiding the behavior. For this reason, future studies will investigate the functional properties of snapper claw mechanoreceptors.

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